EVALUATING HARD RED AND WHITE SPRING WHEAT (TRITICUM AESTIVUM L.) GENOTYPES FOR TOLERANCE TO PRE-HARVEST SPROUTING

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By

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ABSTRACT

Each genotype was exposed to controlled PHS conditions for evaluation of susceptibility or tolerance to sprouting, falling number, kernel color, test weight, and yield. The 24 genotypes were grown in replicated trials at three locations over three years, all data subjected to an analysis of variance.

Over three years the genotypes were rated for visual PHS using a 1 to 9 scale, with 1 equivalent to no visual PHS and 9 equivalent to maximum visual PHS. The red genotypes exhibited a higher tolerance to PHS than white genotypes with a mean PHS score of 4.46 compared with 5.16 for white genotypes. Not all the white genotypes were equally susceptible to PHS or more susceptible than the red genotypes, suggesting that not all seed dormancy is linked to the kernel color genes.

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INTRODUCTION

When physiologically mature grain is exposed to high humidity or rain before harvest, the grain can germinate in the spike. Pre-harvest sprouting (PHS) in wheat (*Triticum aestivum L.)* is a major constraint to the production of high-quality grain, and it makes the grain unusable for many products. Starch is the primary component of grain, and alpha-amylase activity has a direct effect on starch degradation. Excessive alpha-amylase activity caused by PHS can degrade starch and result in poor end-use quality of wheat products. PHS damage results in reduced flour water absorption, which reduces the number of loaves of bread produced from a given amount of flour (Dexter and Edwards, 2003)

Due to an emphasis on whole-grain products, the domestic and international milling and baking industries are encouraging the production of white wheat throughout the Northern Plains and entire U.S. The demand for whole-grain milled products is increasing, and the flour resulting from milling white wheat produces lighter color bread preferred by many consumers when compared with the flour produced from red wheat. However, red wheat generally exhibits a higher level of tolerance to PHS when compared with white wheat. Extensive research has shown that there is a strong association between tolerance to PHS and the genes that determine the red kernel color in wheat (Groos et al., 2002).

To effectively develop hard white spring wheat cultivars with tolerance to PHS, it is important for plant breeders in the Northern Plains to know the range of tolerance expressed by adapted genotypes and if white kernel genotypes are generally more susceptible to PHS. Hence, the objectives of this study were to 1) evaluate a cross-section of adapted hard red and white spring wheat cultivars for their reactions to PHS, and 2) determine the relationship between kernel brightness PHS tolerance, and falling number.

LITERATURE REVIEW

Most hard red spring wheat (HRSW) cultivars have been selected such that they exhibit a high level of tolerance to PHS. Nevertheless, PHS damage can result in substantial losses in the spring wheat growing region and in other areas throughout the world (Flintham et al., 2000). Although there is considerable variability in the level of tolerance to PHS in wheat, in striving for tolerance, breeders must also be concerned with seed dormancy and inhibiting germination, since PHS is closely related to dormancy (Bewely, 1997).

Germination encompasses events that commence with the uptake of water by the quiescent dry seed and terminate with the elongation of the embryonic axis (Bewely, 1997), while seed dormancy is defined by the temporary failure of a viable seed to germinate after a specific length of time when the seed is exposed to a favorable set of environmental conditions (Bewely, 1997). Dormancy is determined by two different factors, one that is coat-imposed and another that is embryo-imposed (Flintham et al., 2000). Coat-imposed dormancy exists when the embryo fails to germinate due to the surrounding seed coat, while embryo-dormancy induces the embryo itself to remain dormant (Bewely, 1997). Embryo dormancy is likely the most beneficial type of dormancy. If dormancy is coat imposed, the embryo may still convert endosperm starch into sugar during sprouting, thus utilizing seed nutrients and affecting end-use product quality.

Environmental factors affect the expression of PHS and make the selection of resistant cultivars difficult. The main environmental factors that impact dormancy are rainfall, high relative humidity, and temperature. Heyne et al. (1987) determined that the optimal amount of moisture for germination in wheat is 35 to 45% of kernel dry weight, and germination may occur at temperatures between 4 and 37˚ C, with 12 to 25˚C considered an optimum temperature range.

There are other factors that contribute to seed dormancy. Temperature and drought conditions during grain-fill are believed to contribute to the level of seed dormancy at maturity. Low temperatures during seed development and grain-fill can prolong dormancy, while low temperatures during germination breaks dormancy in freshly harvested seeds (Nyachiro et al., 2002). Irrigated trials grown under low temperatures produced a similar level of dormancy when compared with high temperature drought-induced trials (Biddulph et al., 2005). However, low-temperature drought induced trials showed the greatest level of seed dormancy (Biddulph et al., 2005).

Wu and Carver (1999) noted that differences in PHS damage are evident between hard red and hard white genotypes at harvest maturity. Damage that was measured as a percentage of sprouted kernels was hardly noticeable among the hard red genotypes, but easily detected among the hard white genotypes. When harvest was delayed, sprout damage was more evident among all genotypes, yet the hard white genotypes showed higher overall PHS damage compared with the hard red genotypes.

There have been numerous studies to identify markers and microsatellites associated with PHS tolerance and seed dormancy. Most of the markers are closely related to the genes determining red kernel color. These genes responsible for red kernel color are located to the long arms of the 3A, 3B, and 3D chromosomes (Bassoi and Flintham, 2005). Red wheat genotypes express a wider range of variation for kernel dormancy and an elevated level of kernel dormancy/tolerance to PHS when compared with white wheat. This suggests that red genotypes carry one or more alleles for kernel dormancy that are not present in white wheat genotypes. Flintham et al. (2002) described a dormancy gene, *Vp1* controlled by triplicate *R* homoeoloci on the long arms of the group-3 chromosomes of wheat. The dominant color gene alleles act in an

additive manner to influence seed dormancy, and as a consequence of this, white wheat genotypes require other genes for adequate dormancy (Groos et al., 2002). Himi et al. (2002) stated that the *R* gene might only act as a minor factor in seed dormancy, and Wu and Carver (1999) acknowledged that the range in resistance among hard red cultivars did not appear to be related to the number of red kernel color genes.

There are markers for PHS tolerance that are not directly related to seed color. Roy et al. (1999) identified a sequence-tagged microsatellite (STMS) on chromosome 6B, and a sequence-tagged site (STS) on chromosome 7D. Their study mapped F_6 inbred lines, and results demonstrated a strong association between each of the markers and tolerance to PHS. They also were able to assign the markers to the associated chromosomes through the use of nulli-tetrasomic lines. In their population, tolerance to PHS was governed by two complementary genes on chromosomes 6B and 7D.

Other potential QTL that are related to seed dormancy, but not with the kernel color genes have been identified on chromosome 4A (Mares et al., 2005). Mares et al. (2005) concluded that the dormancy QTL on chromosome 4A alone is not sufficient to produce progeny with a level of dormancy equivalent to the most dormant parent, and doubled-haploid lines that contained the 4A QTL allele from the dormant parent only expressed an intermediate level of dormancy.

Mares et al. (2005) confirmed the location of QTL for PHS tolerance, and these QTL were identified in other studies (Flintham et al., 2000; Flintham et al., 2002). A major gene for wheat grain dormancy, *Phs*, which is thought to affect the embryo was originally located to chromosome 7D (Flintham et al., 2000). However, the true location of the gene is on the long arm of 4A (Flintham et. al., 2002). Flintham (2000) suggested that expression of *Phs* was stable

over two years of field trials, and that its expression accounted for the majority of the phenotypic variance in their population. The gene is semi-dominant, and its expression is independent of the seed coat and expression of the color genes. Still, the effect of *Phs* on dormancy appears to be comparable to that of the color genes.

Many morphological spike features may impact expression of PHS. Cultivars with awns absorbed up to 30% more water than their awnless counterparts, and awnless cultivars showed a higher level of tolerance to PHS (King and Richards, 1984).

In addition to the presence/absence of awns, the pericarp or fruit coat thickness may play an important role in the tolerance to PHS. The pericarp surrounds the entire seed and is composed of several layers. The layers of the pericarp from the outside inward are: epidermis, hypodermis, cross cells, tube cells, seed coat (testa), nucellar tissue, and aleurone cell wall (Hoseney, 1998). The thickness of the seed coat can vary from 5 to 8 μm (Hoseney, 1998). The seed coat consists of three layers: a thick outer cuticle, a layer that either contains or does not contain pigment, and a thin inner cuticle (Hoseney, 1998). The seed coat of white wheat has two compressed cell layers of cellulose containing little or no pigment (Hoseney, 1998). In red wheat, the testa layer or seed coat contains pigments that prevent pre-mature germination (Zakowesky et al., 2005). Differences among the seed coat or testa layer may be an indicator of susceptibly to PHS.

It has been suggested that there may be differential water uptake due to the amount of nucellar lysate between the nucellar tissue and the seed coat (Evers and Reed, 1988). The lack of the pigment layer in the seed coat of white wheat, and the lysate between the nucellar tissue may be a primary cause for their general higher level of susceptibility to PHS.

Starch is the predominant component of wheat grain, and alpha-amylase activity has a direct effect on starch degradation. Alpha-amylase is an enzyme that breaks down starch to sugars. Specifically, alpha-amylase is an enzyme that breaks glucosidic bonds, which results in a decrease in the size of large starch molecules (Hoseney et al., 1998). Therefore, non-sprouted cereal grain expresses a relatively low level of alpha-amylase activity, but all grain exhibits some level of alpha-amylase activity. Upon germination however, the level of alpha-amylase activity increases significantly, and elevated alpha-amylase activity decreases the viscosity of starch in a solution or slurry (Hoseney et al., 1998).

Other factors can contribute to elevated levels of alpha-amylase activity not caused by PHS. Mares et al. (2008) indicated that late maturity a-amylase (LMA), or prematurity a-amylase (PMAA) as it has been termed in the UK, in wheat involves the synthesis of high alpha-amylase during the middle to later stages of grain development and ripening.

Elevated alpha-amylase activity degrades starch and reduces the baking quality of flour. The result of alpha-amylase on starch is a reduction in the water holding capacity of the starch. This leads to a reduction in the water absorption capacity of flour, and it reduces the number of loaves of bread produced from a given amount of flour (Dexter and Edwards, 2003). Another consequence is that the flour produces sticky dough, which causes handling problems for bakers (Every and Ross, 1996). The sticky crumb also makes the bread hard to slice, since the crumb builds up on slicing blades (Dexter and Edwards, 2003).

OBJECTIVES AND HYPOTHESIS

The objectives of this study were to 1) evaluate a representative regionally adapted group of hard red and white spring wheat genotypes for their reaction to PHS, and 2) determine the extent of the relationship between kernel color and tolerance to PHS in these genotypes.

Ho_1: The PHS tolerance of red and white genotypes will not be significantly different.

Ho_2: There is no relationship between kernel color and susceptibility or tolerance to PHS.

MATERIALS AND METHODS

Plant Materials

Twenty-four genotypes representing 12 red and 12 white spring wheats, including cultivars typically produced in the spring wheat region of the U.S. were evaluated (Table 1). 'Hanna' and 'AC Snowbird' have previously demonstrated a high level of seed dormancy (Smith, 2006). Consequently, Hanna was considered a red kernel control for tolerance to PHS, and AC Snowbird a white kernel control. 'Ingot' and 'Lolo' which were previously shown to exhibit susceptibility to PHS (Anderson, 2006) were considered PHS susceptible red and white kernel types, respectively.

Methods

Experiments were arranged in a randomized complete block design with four replications and they were conducted over three years, 2006 to 2008. In each year, experimental plots were grown at Prosper, Carrington, and Casselton, ND. The experimental unit consisted of a four-row plot planted at a seeding rate of 81.8 kg per ha^{-1}, with a length of 3.0 m. Rows were spaced 30.5 cm apart, and plots were trimmed to 2.4 m x 1.2m prior to harvest. The soil types at the Prosper and Casselton are similar. They are classified as a Perella-Bearden silty clay loam, which consists of level, deep somewhat poorly drained soil type. The soil type at Carrington is classified as a Heimdal-Emrick loam, which is a very deep, level soil. Typically, runoff is slow for such a soil, although permeability is moderate and available water holding capacity is high.

Plots were sprayed with a backpack sprayer twice each season when plants were at Feekes stage 5.0 and 9.0 with a propiconazole fungicide at a rate of 292.3 ml ha^{-1}. These treatments were to control tan spot (*Pyrenophora tritici-repentis*), and leaf rust (*Puccinia triticina*) diseases, which may have obscured accurate determinations of kernel brightness and

quality. For control of *Fusarium* head blight, a tebuconazole fungicide was similarly applied at Feekes stage 10.5 at a rate of 292.3 ml ha^{-1}. When possible, rainfall amounts and average temperatures were recorded at the locations for the months of the season when the experiments were growing.

DATA COLLECTION AND SAMPLING

Preharvest Sprouting

Genotypes were evaluated for tolerance to PHS after exposing a sub-sampling of spikes harvested from individual plots to high moisture in a mist chamber. At physiological maturity, 30 spikes were randomly harvested from each experimental plot. The spikes were immediately stored at 10^{o} C to inhibit additional alpha-amylase activity, and later placed in a mist chamber and misted for a period of 48 h. Following misting, the spikes were maintained at constant high humidity by placing a humidifier in the chamber for 3 d. Visual observations of the spikes were made, and they were rated for germination using a 1 to 9 scale, with 1 representing spikes showing no visual germination and 9 representing spikes showing nearly 100% germination (Table 2).

Grain Color

Immediately after harvesting plots, a 50 g sub-sample of seed was taken from each plot and stored at -10^{o} C. A Minolta colorimeter was used to measure kernel color of the sub-samples. Sub-samples were classified as white or red according to established criteria (Peterson et al., 2001), and colorimeter measurements were made based on a standard color space scale (CIE, 1976), where white wheat kernels typically measure 50 or above on the L* brightness scale and a reading of 100 is equivalent to pure white. Red wheat kernels typically measure less than 50 on the L* brightness scale, where a value of 0 represents pure black.

Falling Number

Falling number measurements represent an indirect measurement of alpha-amylase activity in grain. A portion of the 50 g sub-sampling of seed from genotypes was used to

measure falling number. Grain samples were ground using a Udy grinder, and falling number readings were made in accordance with the AACC approved method (AACC, 1999).

Yield and Grain Volume Weight

Remaining plot seed was harvested using a small-plot combine, and genotypes were evaluated for grain yield and grain volume weight (GVW). GVW was determined by using a pint measuring cup according to approved AACC method 55-10 (AACC, 1999?).

Table 1. Hard red spring (HRS) and hard white spring (HWS) genotypes included in the study, their class, year, origin of release, and their pedigrees.

		Genotype Information		
Class	**Genotype**	**Year**	**Origin**	**Pedigree**
HRS	Alsen	2000	NDSU	ND674//ND2710/ND688,
HRS	Briggs	2002	SDSU	AC Pasua/Bergen//SD3097
HRS	Freyr	2004	AgriPro	Sonja/Vance//Sumai#3/Dalen
HRS	Glenn	2005	NDSU	Sumai3/Wheaton//Grandin/ND688/3/Steele-ND
HRS	Granite	2002	WPB	ACSS4m-k/3/LNL/TG/312S
HRS	Hanna	2002	AgriPro	MN70170/ECM403//Katepwa/3/Benito/4/AC Domain
HRS	Knudson	2002	AgriPro	Karl/Krona/3/Bergen//Erik/MN73167
HRS	Ingot	1998	SDSU	SD3080/Dalen (SD3080 = Butte 86/SD3004)
HRS	Kelby	2005	AgriPro	N97-0117/N92-0098//Sumai#3/Dalen
HRS	Norpro	1999	AgriPro	88-0436/Dalen
HRS	Steele-ND	2003	NDSU	Parshall/ND706
HRS	Reeder	1999	NDSU	IAS20*4/HH567.71//Stoa/3/ND674
HWS	Snowbird	2004	Canada	RL4137*6//TC/POSO48//AC Domain
HWS	AC Vista	1996	Canada	HY344/7915-QX76B2/HY358*3/BT10
HWS	Argent	1998	NDSU	Grandin*5/ND614
HWS	Diamond	2005	Canterra	AUS1408//Kokako/CSW1889/Endeavour
HWS	Peerless	2005	Canterra	Otane/AC Karma
HWS	Explorer	2001	MSU	MT8182/Fortuna//Pondera/MT8182
HWS	Lolo	1997	U of I	A9158S//Oasis 86/IDO377
HWS	MT9420	2001	MSU	MT8182/MT8289
HWS	NDSW0602	Exp	NDSU	N97-0117//MT9420/3/971//IDO533/9747
HWS	Otis	2005	WSU	(PI 591045)/3/Tanager3/Torim73
HWS	Pristine	2001	WPB	Fergus/Golden 86
HWS	99S0155-14W	Exp	AgriPro	Ivan/2/Haqmer//Sumai3/Dalen

Table 2. Scale to visually evaluate spring wheat spikes for PHS.

Score	Description
1	Visible radicles emerging from approximately 10% of spikelets.
2	Visible radicles emerging from approximately 20% of spikelets.
3	Visible radicles emerging from approximately 30% of spikelets.
4	Visible radicles emerging from approximately 40% of spikelets.
5	Visible radicles emerging from approximately 50 to 100% of spikelets. Coleoptiles emerging from 10 to 20% of spikelets.
6	Visible radicles emerging from approximately 50 to 100% of spikelets. Coleoptiles emerging from 30 to 40% of spikelets.
7	Visible radicles emerging from approximately 50 to 100% of spikelets. Coleoptiles emerging from 50 to 100% of spikelets. Average coleoptile length less than 1 cm.
8	Visible radicles emerging from approximately 50 to 100% of spikelets. Coleoptiles emerging from 50 to 100% of spikelets. Average coleoptile length 1 to 2 cm.
9	Visible radicles emerging from approximately 50 to 100% of spikelets. Coleoptiles emerging from 50 to 100% of spikelets. Average coleoptile length greater than 2 cm.

Fig. 1. Representative photo of spikes exhibiting tolerance to PHS (score = 1).

Fig. 2. Representative photo of spikes exhibiting susceptibility to PHS (score = 9).

Table 3. Analysis of variance table of a RCBD experiment with 24 genotypes and 4 replications at a single environment.

Source of Variation	Degrees of Freedom	Expected Mean Square
Replication	3	$\sigma^2 + r\sigma g^2 + g\sigma r^2$
Genotype	23	$\sigma^2 + r\sigma g^2$
Error	69	σ^2
Total	95	

Table 4. Combined analysis of variance table of a RCBD experiment with 24 genotypes and 4 replications at three environments.

Source of Variation		Degrees of Freedom	Expected Mean Square
Environments	e-1	2	
Reps/Environment	(r-1)e	9	
Genotype	g-1	23	$\sigma^2 e + r\sigma^2 ge + re\sigma^2 g$
G X E	(g-1)(e-1)	46	$\sigma^2 e + r\sigma^2 ge$
Error	(g-1)(r-1)e	207	$\sigma^2 e$
Total		287	

RESULTS AND DISCUSSION

Environmental Conditions

Environmental conditions in 2006, 2007, and 2008 represented the wide range of variability for temperature and rainfall that can be expected at the various experimental locations (Table 5). Each location received lower than normal precipitation in the early part of the growing seasons in 2006 and 2008. Conversely, in 2007 all locations received a higher than normal amount of precipitation during May. Temperatures in 2006 were normal compared to long-term averages. Temperatures in 2007 at Carrington and Prosper, were above normal, but below normal at both environments in 2008.

Kernel Brightness

With significant results across the nine environments, a Bartlett's chi-square test of homogeneity indicated not all variances were homogenous, therefore, not all locations were combined for colorimeter L* value. Seven environments were combined with a χ^2 value of 72.8; whereas, the 2008 Casselton and 2006 Prosper variances were combined with a χ^2 value of 6.4, and analyzed separately. The mean colorimeter L* value over seven environments was 49.5; whereas, the 2008 Casselton and 2006 Prosper mean was 48.5 .

Results in Tables 6 and 7 indicate that genotype, and genotype x environment interaction were highly significant for L* value. Glenn had the lowest mean L* value across all environments, which suggests that Glenn likely is homozygous for the three dominant *R* genes (Table 8).

The range of colorimeter L* values for the genotypes suggests that in addition to the genes responsible for kernel color, other factors impact kernel brightness. Studies have indicated that a delayed harvest can result in bleaching of the kernel (Gan et al., 2000). Additionally, the

range of L* values may indicate that not all of the red genotypes possess 3 homozygous alleles for kernel color.

Table 5. Weather data for the growing seasons of 2006, 2007 and 2008 at Carrington, and Prosper, North Dakota.

		Precipitation		Temperature			
Environment	Month	Total	%Normal†	Max.	Min	Avg.	±Normal†
		mm		°C			
Carrington 2006	May	29	46	20	7	14	0
	June	88	92	25	12	19	+1
	July	27	34	30	14	22	+1
	Aug.	54	86	28	12	20	0
Carrington 2007	May	136	295	20	7	14	0
	June	66	84	33	21	27	+9
	July	85	116	29	15	22	+1
	Aug.	85	190	24	12	18	-2
Carrington 2008	May	30	48	18	2	10	-4
	June	127	132	22	10	16	-2
	July	47	59	27	14	20	0
	Aug.	39	62	27	12	20	-1
Prosper 2006‡	May	41	60	20	7	14	+1
	June	12	13	25	12	19	+1
	July	66	80	30	15	22	+1
	Aug.	25	37	27	13	20	0
Prosper 2007‡	May	123	181	22	9	15	+2
	June	106	116	27	14	21	+3
	July	49	60	29	15	22	+1
	Aug.	48	71	24	11	18	-2
Prosper 2008‡	May	38	57	20	4	12	-1
	June	164	180	23	11	17	-1
	July	75	91	27	14	20	0
	Aug.	77	113	28	13	20	0

† Based on 1971-2007 average.

‡ Due to the proximity of the location, data used for Casselton

Furthermore, the range of L* values among the white genotypes may indicate the involvement of alleles other than those for the genes related to kernel color, and it likely indicates that environment also affects L* values.

Glenn had the lowest mean kernel brightness readings, with a mean L* value of 46.80 over the seven locations, and a mean value of 45.46 over the two environments. Explorer had the highest mean kernel brightness with a reading of 53.16 over the seven environments and 51.97 over the two environments (Table 8).

Argent displayed the lowest L* mean for a white genotype at 49.46 and 49.30 over the seven and two environments, respectively. Matus-Cádiz et al. (2008) noted that Argent did not meet the USDA Federal Grain Inspection Service (FGIS) color standards as a white wheat, and thus, it was classified by the FGIS as a hard red spring wheat. Matus-Cádiz et al.,(2008) concluded that higher free phenolic compounds in the bran of Argent could explain why seed of Argent is darker than expected for a white wheat cultivar. In the present study, neither the red or white wheats were genotyped with markers or otherwise confirmed as being homozygous dominant or recessive for the major color genes. Genotypic variation for the major genes as well as the phenotypic expression of phenolics in the bran similar to Argent are two possible reasons for the differences in measured kernel L* values.

Results in Table 9 indicate the mean L* value over seven environments was significant. The 2006 L* value was the highest at 50.56; whereas, the 2007 Carrington L* value was the lowest, at 49.19. The differences between environments demonstrate the environmental impact on L* values. Matus-Cádiz et al (2003) noted that genotypic differences in grain brightness was generally stable across environments, however hard white kernels tended to be smaller and appear more red in dry years. Additionally, Peterson et al. (2001) suggested that

environmentally induced variations in grain protein content, hardness, vitreousness, and kernel size and shape might all contribute to variation in visual grain color.

Results in Table 10 indicate that, 2006 Prosper, and 2008 Carrington had lower mean L* values when compared to the other seven environments. With the exception of June at Carrington, 2008, both environments had lower than average precipitation. Any delay of harvest after physiological maturity can greatly impact seed coat color (Gan et al., 2000). The genotypes tested displayed a range of maturities, which depending on the environment, may have impacted L* values.

Table 6. Combined analysis of variance table for L* across seven locations.

Source of Variation	Degrees of Freedom	Mean Square
Environments	6	17.8**
Reps/Environment	21	1.5**
Genotype	23	129.6**
G X E	138	1.7**
Error	483	.42
CV%		1.3%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 7. Combined analysis of variance table for L* across two locations.

Source of Variation	Degrees of Freedom	Mean Square
Environments	1	5.4*
Reps/Environment	6	5.4
Genotype	23	39.3**
G X E	23	2.2
Error	276	1.4
CV%		2.4%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 8. Mean L* values across seven and two North Dakota environments respectively during 2006, 2007, and 2008.

Genotype	Mean	Genotype	Mean
	Colorimeter L Value		
ALSEN	47.3	ALSEN	46.2
BRIGGS	48.0	BRIGGS	46.8
FREYR	46.8	FREYR	46.0
GLENN	46.8	GLENN	45.5
GRANITE	47.1	GRANITE	46.4
HANNA	48.0	HANNA	47.0
INGOT	48.2	INGOT	47.1
KELBY	48.1	KELBY	46.7
KNUDSON	47.4	KNUDSON	46.8
NORPRO	46.9	NORPRO	46.1
REEDER	48.5	REEDER	46.7
STEELE-ND	47.5	STEELE-ND	46.1
99S0155-14-1W §	51.8	99S0155-14-1W §	50.9
AC SNOWBIRD §	50.7	AC SNOWBIRD §	49.4
AC VISTA §	51.7	AC VISTA §	50.9
ARGENT §	49.5	ARGENT §	49.3
DIAMOND §	51.7	DIAMOND §	51.6
PEERLESS §	52.3	PEERLESS §	50.9
EXPLORER §	53.2	EXPLORER §	52.0
LOLO §	51.4	LOLO §	50.8
MT9420 §	52.3	MT9420 §	51.4
NDSW0602 §	50.9	NDSW0602 §	49.7
OTIS §	51.5	OTIS §	50.2
PRISTINE §	51.0	PRISTINE §	49.6
MEAN	49.5	MEAN	48.5
LSD (5%)	0.3	LSD (5%)	1.2

§ Denotes white genotypes.

Table 9. Mean L* values averaged across seven North Dakota environments during 2006, 2007, and 2008.

Year	Location	Mean
2006	Carrington	50.6
2006	Casselton	49.5
2007	Carrington	49.2
2007	Casselton	49.5
2007	Prosper	49.8
2008	Casselton	49.7
2008	Prosper	49.5
	LDS (5%)	.2

Table 10. Mean L* values across two North Dakota environments during 2006, 2007, and 2008.

Year	Location	Mean
2006	Prosper	48.3
2008	Carrington	48.7
	Mean	48.5
	LDS (5%)	.3

Preharvest Sprouting

Environmental variances were significant, and a Bartlett's chi-square test of homogeneity indicated that the environmental variances were homogenous, $\chi^2 = 69.7$. Therefore ,all environments were combined for the evaluation of PHS. Data analysis of PHS showed the environment, genotype, and genotype x environment were all highly significant for PHS (Table 11).

The mean PHS score over all nine environments was 4.8, and scores for genotypes over environments ranged from 2.22 for 99S0155-14-1W, a white kernel genotype, to 6.64 for Explorer, also a white kernel genotype (Table 12). The susceptible control genotypes, Ingot and Lolo, had mean PHS scores of 6.44 and 5.17, respectively (Table 12). The tolerant control genotypes, Hanna and AC Snowbird had means scores of 2.72 and 2.47, respectively(Table 12).

Two white kernel genotypes, 99S0155-14W, and AC Snowbird both were the most tolerant to PHS, but the mean PHS score for white genotypes over all environments was 5.16.

In comparison, the PHS mean for the red kernel genotypes was 4.46. Although some white kernel genotypes are more tolerant than the most tolerant red genotypes, on average, the white genotypes were more susceptible than the red genotypes. Similarly, there were red genotypes that exhibited very little tolerance to PHS. For example, Ingot was the third most susceptible to sprouting under PHS conditions. However, Knudson, NorPro, and Granite exhibited PHS scores higher than the mean.

Additionally morphological characteristics may play an important role in PHS tolerance. AC Snowbird is an awnless cultivar, and displayed a very high level of tolerance to PHS. Cultivars with awns absorbed up to 30% more water than their awnless counterparts, and awnless cultivars showed a higher level of tolerance to PHS (King and Richards, 1984).

Furthermore Derera et al. (1977) demonstrated differential sensitivity of wheat cultivars to germinate in the presence of their chaff or tissue. Wu et al. (1999) demonstrated that with the addition of chaff extract to the germination medium, seed germination was inhibited by 20 to 85% of germination without the extract. Both Glenn and Hanna displayed high levels of tolerance to PHS. Seed of these two genotypes is generally more difficult to thresh from the spikes at maturity in comparison to other genotypes. This may indicate that not only chaff tissue can inhibit germination, but glume structure and adherence of the glume to the kernels may provide a barrier to moisture reaching the kernels under PHS conditions.

Mean PHS score was the highest at Carrington, 2008, and 2006 Prosper had the lowest PHS score (Table 13). Biddulph et. al (2005) indicated that high temperatures with drought conditions resulted in seed with a high level of dormancy. The 2006 growing season was the driest of the three years (Table 5), which may have contributed to the lower PHS scores for that year.

Table 11. Combined analysis of variance table for PHS values across nine locations

Source of Variation	Degrees of Freedom	Expected Mean Square
Environments	8	44.5**
Reps/Environment	27	2.0
Genotype	23	62.0 **
G X E	184	2.31 **
Error	621	1.4
Total	863	
C.V.%		24.13

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 12. Mean PHS values averaged across nine North Dakota environments during 2006, 2007, and 2008.

Genotype	Sprout Value
ALSEN	4.1
BRIGGS	4.5
FREYR	4.2
GLENN	3.4
GRANITE	5.5
HANNA	2.7
INGOT	6.4
KELBY	3.6
KNUDSON	5.2
NORPRO	5.8
REEDER	4.2
STEELE-ND	4.3
99S0155-14-1W §	2.2
AC SNOWBIRD §	2.5
AC VISTA §	5.7
ARGENT §	4.3
DIAMOND §	6.4
EXPLORER §	5.2
LOLO §	6.1
MT9420 §	5.7
NDSW0602 §	6.5
OTIS §	6.1
PEERLESS §	6.6
PRISTINE §	4.4
MEAN	4.8
LSD (5%)	0.5

§ Denotes white genotypes.

Table 13. Mean PHS values ranked by location from lowest to highest, averaged across nine North Dakota environments during 2006, 2007, and 2008.

Year	Location	Mean Location Sprout Value
2008	Carrington	6.0
2008	Casselton	5.3
2007	Carrington	5.2
2007	Casselton	5.1
2007	Prosper	5.1
2008	Prosper	4.5
2006	Carrington	4.2
2006	Casselton	4.2
2006	Prosper	3.8
	Mean	4.8
	LDS (5%)	.3

Falling Number

While the individual environmental analysis proved to be significant, a Bartlett's chi-square test of homogeneity indicated not all variances were homogenous; therefore, not all environments were combined for analyses of falling number. With a χ^2 value of 69.7, the five environments; 2006 Prosper, 2006 and 2008 Casselton, and 2006 and 2007 Carrington were in the ANOVA, and environment, genotype, and genotype x environment interactions were highly significant (Table 14). After combining the other environments; 2007 and 2008 Prosper, 2007 Casselton, and 2008 Carrington in the ANOVA, environment, genotype, and genotype x environment interactions were highly significant with a χ^2 value of 40.8 (Table 15). The mean falling number value over five environments was 488.6 s; whereas, over four environments, it was 586.2 s (Table 16).

Wu et al. (1999) stated that a falling number of greater than 300 s serves as minimum for predicting that wheat grain is not exhibiting PHS, while anything less is predictive of grain that has sprouted. Although differences were seen among the genotypes tested in the present study

(Table 16), all falling number values for genotypes were above 300 s, indicating little PHS damage prior to harvest.

At 577.7s, Briggs had the highest mean falling number value over the five environments. Norpro had the highest mean falling number over the four environments at 737.5 s. At 421.9 s MT9420 had the lowest mean falling number value over the five environments, while Explorer had the lowest mean over the four environments at 472.8 s. While significant differences were observed among the genotypes, all genotypes displayed no PHS damage prior to harvest. However, falling number differences among the genotypes may be related to late maturity alpha-amylase activity (Mares et al 2008).

Similar to the individual genotypic results, the mean falling number for all white genotypes was 471.3 s; whereas, that for the red genotypes was 505.4 s. The mean for the white genotypes over four environments was 538.4 s; whereas, the mean for red genotypes was 624.5 s. While genotypes that display lower falling number values may also be susceptible to PHS, falling number was not always predictive or indicative of PHS. Glenn had a mean falling number value lower than the mean of the red genotypes, but Glenn expressed a high level of tolerance to PHS (Table 12). This could be an indicator that Glenn is more susceptible to late maturity alpha-amylase activity.

Means of the environments were significantly different (Tables 17 and 18). The five-year environment mean was 490.37 s; whereas, the four-year environment mean was 591.16 s**.** Wu et al, (1999) stated falling number values can fluctuate widely depending on the degree of ripening and the amount of rainfall preceding harvest. While there are genotypic differences for falling number, environmental differences can affect falling number values.

Table 14. Combined analysis of variance for falling number across five locations.

Source of Variation	Degrees of Freedom	Mean Square
Environments	4	49,5516.7**
Reps/Environment	15	3185.9
Genotype	23	35,272.1**
G X E	92	14,204.8**
Error	345	2437.3
CV%		10.1%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.
† L = 100 (white) to 0 (black)

Table 15. Combined analysis of variance for falling number across four North Dakota environments over 2007 and 2008.

Source of Variation	Degrees of Freedom	Mean Square
Environments	3	1569297.2**
Reps/Environment	12	7694.9
Genotype	23	89022.1**
G X E	69	19380.4**
Error	276	12248.0
CV%		18.9%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 16. Mean falling number values averaged across five and four North Dakota environments respectively during 2006, 2007, and 2008.

Genotype	Five Location Mean	Genotype	Four Location Mean
	Seconds		Seconds
ALSEN	490.4	ALSEN	589.9
BRIGGS	577.7	BRIGGS	686.4
FREYR	553.1	FREYR	725.0
GLENN	480.1	GLENN	530.5
GRANITE	434.1	GRANITE	622.9
HANNA	498.5	HANNA	653.2
INGOT	503.2	INGOT	616.7
KELBY	518.1	KELBY	639.0
KNUDSON	523.7	KNUDSON	576.9
NORPRO	511.0	NORPRO	737.5
REEDER	487.8	REEDER	596.0
STEELE-ND	492.5	STEELE-ND	632.6
99S0155-14-1W §	489.9	99S0155-14-1W §	550.0
AC SNOWBIRD §	545.2	AC SNOWBIRD §	635.0
AC VISTA §	525.3	AC VISTA §	614.6
ARGENT §	483.8	ARGENT §	584.8
DIAMOND §	497.6	DIAMOND §	506.1
EXPLORER §	431.2	EXPLORER §	472.8
LOLO §	422.2	LOLO §	501.1
MT9420 §	421.9	MT9420 §	478.2
NDSW0602 §	478.2	NDSW0602 §	576.6
OTIS §	427.7	OTIS §	475.4
PEERLESS §	445.5	PEERLESS §	541.0
PRISTINE §	487.8	PRISTINE §	525.9
MEAN	488.6	MEAN	586.2
LSD (5%)	30.7	LSD (5%)	77.0

§ Denotes white genotypes.

Table 17. Mean falling number averaged across five North Dakota environments during 2006, 2007, and 2008.

Year	Location	Mean Location FN Value
2006	Carrington	515.6
2006	Casselton	440.1
2006	Prosper	443.8
2007	Carrington	602.6
2008	Casselton	449.8
	Mean	490.4
	LDS (5%)	14.0

Table 18. Mean falling number values averaged across four North Dakota environments during 2006, 2007, and 2008.

Year	Location	Mean Location Sprout Value
2007	Casselton	667.22
2007	Prosper	722.29
2008	Carrington	484.27
2008	Prosper	490.86
	Mean	591.16
	LDS (5%)	31.44

Grain Yield

A Bartlett's chi-square test of homogeneity indicated not all variances were homogenous, therefore not all environments were combined for grain yield. Eight environments were combined with a χ^2 value of 60.7, while 2006 Carrington data were analyzed separately. Results of the ANOVA for grain yield (Table 19) indicate the main factors of environment and genotype, and the genotype by environment interactions were highly significant. In 2006, genotype was highly significant (Table 20).

In evaluating red and white genotypes, Peterson et al. (1992) reported a significant genotype by environment interaction for grain yield. In the present study, the red genotypes generally expressed higher grain yields when compared to the white genotypes (Table 21). Reeder, a HRSW, expressed the highest yield potential across the eight environments and

Carrington in 2006 ,yielding 3761.2 kg ha^{-1} and 1820.5 kg ha^{-1}, respectively. Conversely, Pristine a HWSW expressed the lowest yield potential across the eight environments yielding 2452.2 kg ha^{-1}. Additionally, Lolo, a HWSW expressed the lowest yield at Carrington during 2006, yielding 964.8 kg ha^{-1}.

The eight environment mean grain yield of the red genotypes was 3413.7 kg ha^{-1}; whereas, the mean for the white genotypes was 3048.1 kg ha^{-1}. This suggests that the regional adaptation of the red genotypes is higher compared with the white genotypes. Similarly, the mean grain yield of red genotypes in the 2006 Carrington environment was higher than the mean grain yield for white genotypes.

The environmental conditions during 2008 provided optimal growing conditions for grain yield (Table 5). Adequate rainfall coupled with below average temperatures during May and June resulted in advantageous early plant development. July and August temperatures remained average to below average, contributing to high grain yield potential.

Conversely, the environmental conditions during 2007 provided the least desirable growing conditions for grain yield (Table 5). Higher than average rainfall in 2007 coupled with above average temperatures during May and June resulted in low grain yield potential. While temperatures remained average for July and August the earlier than normal plant development in 2007 resulted in low grain yields.

The location mean yields were significant (Table 22). The 2008 Casselton location grain yield was the highest, with a mean of 4890.6 kg ha-1.l. Grain yields were the lowest in the 2006 Casselton environment.

Table 19. Combined analysis of variance for grain yield across eight locations.

Source of Variation	Degrees of Freedom	Mean Square
Environments	7	34,283.7**
Reps/Environment	24	245.9**
Genotype	23	835.7**
G X E	161	177.7**
Error	552	62.2
CV. %		16.3%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 20. Analysis of variance for grain yield at Carrington during 2006.

Source of Variation	Degrees of Freedom	Mean Square
Replication	3	74.4**
Genotype	23	41.6**
Error	69	7.1
CV, %		12.3%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 21. Mean yield averaged across eight and one North Dakota environments respectively during 2006, 2007, and 2008.

2006 and 2007 Environments		2008 Carrington Environment	
Genotype	Grain Yield	Genotype	Grain Yield
	kg ha^{-1}		kg ha^{-1}
BRIGGS	3730.6	BRIGGS	1399.3
FREYR	3495.5	FREYR	1667.8
GLENN	3202.4	GLENN	1372.5
GRANITE	3544.5	GRANITE	1303.7
HANNA	3084.9	HANNA	1562.1
INGOT	3607.3	INGOT	1033.6
KELBY	3567.5	KELBY	1724.8
KNUDSON	3365.4	KNUDSON	1726.5
NORPRO	3400.8	NORPRO	1255.0
REEDER	3761.2	REEDER	1820.5
STEELE-ND	3676.6	STEELE-ND	1510.1
99S0155-14-1W §	2951.0	99S0155-14-1W §	1422.8
AC SNOWBIRD §	2836.2	AC SNOWBIRD §	1552.0
AC VISTA §	3605.3	AC VISTA §	1313.8
ARGENT §	2922.3	ARGENT §	1620.8
DIAMOND §	2702.1	DIAMOND §	1510.1
EXPLORER §	3391.4	EXPLORER §	1515.1
LOLO §	3032.2	LOLO §	964.8
MT9420 §	3171.0	MT9420 §	1394.3
NDSW0602 §	3068.9	NDSW0602 §	1432.9
OTIS §	3100.2	OTIS §	1308.7
PEERLESS §	3345.0	PEERLESS §	1552.0
PRISTINE §	2452.2	PRISTINE §	1125.8
MEAN	3254.9	MEAN GENERAL	1447.6
LSD (5%)	259.8	LSD (5%)	251.6

§ Denotes white genotypes.

Table 22. Mean environment yield averaged across eight North Dakota environments during 2006, 2007, and 2008

Year	Location	Mean Location Yield kg ha^{-1}
2006	Casselton	1463.8
2006	Prosper	3973.2
2007	Carrington	2714.1
2007	Casselton	1752.4
2007	Prosper	2720.8
2008	Carrington	4277.9
2008	Casselton	4890.6
2008	Prosper	4244.3
	Mean	2893.0
	LDS (5%)	149.67

Grain Volume Weight

A Bartlett's chi-square test of homogeneity indicated not all variances were homogenous; therefore, not all environments were combined for GVW. Data from eight environments were combined with a χ^2 value of 88.6; whereas, the 2008 Carrington environment was analyzed and is reported separately. Results of the ANOVA for GVW (Table 23) indicate the main factors of environment and genotype, and the genotype by environment interactions were highly significant. Data from 2008 demonstrates that genotype was highly significant (Table 24).

Glenn displayed the highest GVW across the eight environments, with a mean of 80.1 kg hL^{-1} (Table 25). Glenn typically expresses a high GVW (Underdahl et al., 2008). Ingot had the highest GVW at Carrington 2008, while ranking second among genotypes with a 79.6 kg hL^{-1} mean over eight locations..

AC Vista, and AC Snowbird displayed the lowest GVW means across the eight environments and in 2008 at Carrington. Gan et al., (2000) reported that AC Vista has exhibited lower GVW when compared to other cultivars at harvest. The regional adaptation of genotypes may impact their GVW. Both the low GVW lines are Canadian, and are not widely grown throughout North Dakota.

The eight environment GVW mean of the red genotypes was 77.8 kg hL^{-1}; whereas, the mean for the white genotypes was 76.1 kg hL^{-1}. This suggests that the regional adaptation of the red genotypes is higher compared with the white genotypes. Similarly, the mean GVW of red genotypes in the 2006 Carrington environment was higher than the mean GVW for white genotypes.

The location means for GVW were significant (Table 26). The 2008 Casselton test weight was the highest with a mean of 81.44 kg hL suggesting that the 2008 Casselton environment optimized GVW. Casselton 2006 was the lowest in GVW at 72.25 kg hL^{-1}. This additionally confirms that the 2006 Casselton location had the least favorable growing, and grain-fill conditions.

Table 23. Combined analysis of variance for GVW across eight locations.

Source of Variation	Degrees of Freedom	Mean Square
Environments	7	26,882.5**
Reps/Environments	24	94.0**
Genotype	23	1948.2**
G X E	161	156.5**
Error	552	27.9
CV%		1.28%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 24. Analysis of variance for GVW at Carrington during 2008.

Source of Variation	Degrees of Freedom	Mean Square
Replication	3	149.8
Genotype	23	467.3**
Error	69	174.2
CV, %		3.22%

* and ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 25. Mean GVW across eight and one North Dakota environments during 2006, 2007, and 2008.

Eight Location Mean	kg hL	2008 Carrington Mean	kg hL
ALSEN	77.9	ALSEN	77.0
BRIGGS	78.1	BRIGGS	78.8
FREYR	76.6	FREYR	76.7
GLENN	80.1	GLENN	81.1
GRANITE	78.7	GRANITE	78.5
HANNA	77.1	HANNA	75.4
INGOT	79.6	INGOT	81.3
KELBY	77.4	KELBY	79.5
KNUDSON	77.3	KNUDSON	76.8
NORPRO	76.0	NORPRO	76.2
REEDER	76.7	REEDER	75.4
STEELE-ND	78.4	STEELE-ND	75.7
99S0155-14-1W §	76.7	99S0155-14-1W §	79.3
AC SNOWBIRD §	76.6	AC SNOWBIRD §	73.7
AC VISTA §	74.3	AC VISTA §	75.4
ARGENT §	77.2	ARGENT §	77.0
DIAMOND §	75.7	DIAMOND §	77.4
EXPLORER §	75.7	EXPLORER §	76.4
LOLO §	76.4	LOLO §	76.4
MT9420 §	75.1	MT9420 §	76.4
NDSW0602 §	75.2	NDSW0602 §	74.8
OTIS §	76.4	OTIS §	73.9
PEERLESS §	76.0	PEERLESS §	74.6
PRISTINE §	77.4	PRISTINE §	77.1
MEAN	76.9	MEAN	76.9
LSD (5%)	.48	LSD (5%)	3.5

§ Denotes white genotypes.

Table 26. Mean GVW averaged across eight North Dakota environments during 2006, 2007, and 2008

Year	Location	Mean Location GVW kg hL
2006	Carrington	72.3
2006	Casselton	73.7
2006	Prosper	76.6
2007	Carrington	77.7
2007	Casselton	80.7
2007	Prosper	76.0
2008	Casselton	81.4
2008	Prosper	77.1
	Mean	76.9
	LDS (5%)	1.5

Correlations

The correlation between PHS scores and colorimeter L* values was significant for six environments; 2006, 2007, and 2008 Carrington, 2007 and 2008 Prosper, and 2008 Casselton.. A Bartlett's chi-square test of homogeneity indicated that the six environments were homogenous, so they were pooled for the correlations. There was a significant positive correlation between PHS scores and L* values across environments (r=.29, P<0.05 Fig 1). While this is not a strong correlation, it suggests that, the white genotypes generally are more susceptibility to PHS. There would have been a stronger correlation had the two genotypes that were the most resistant to PHS not been white.

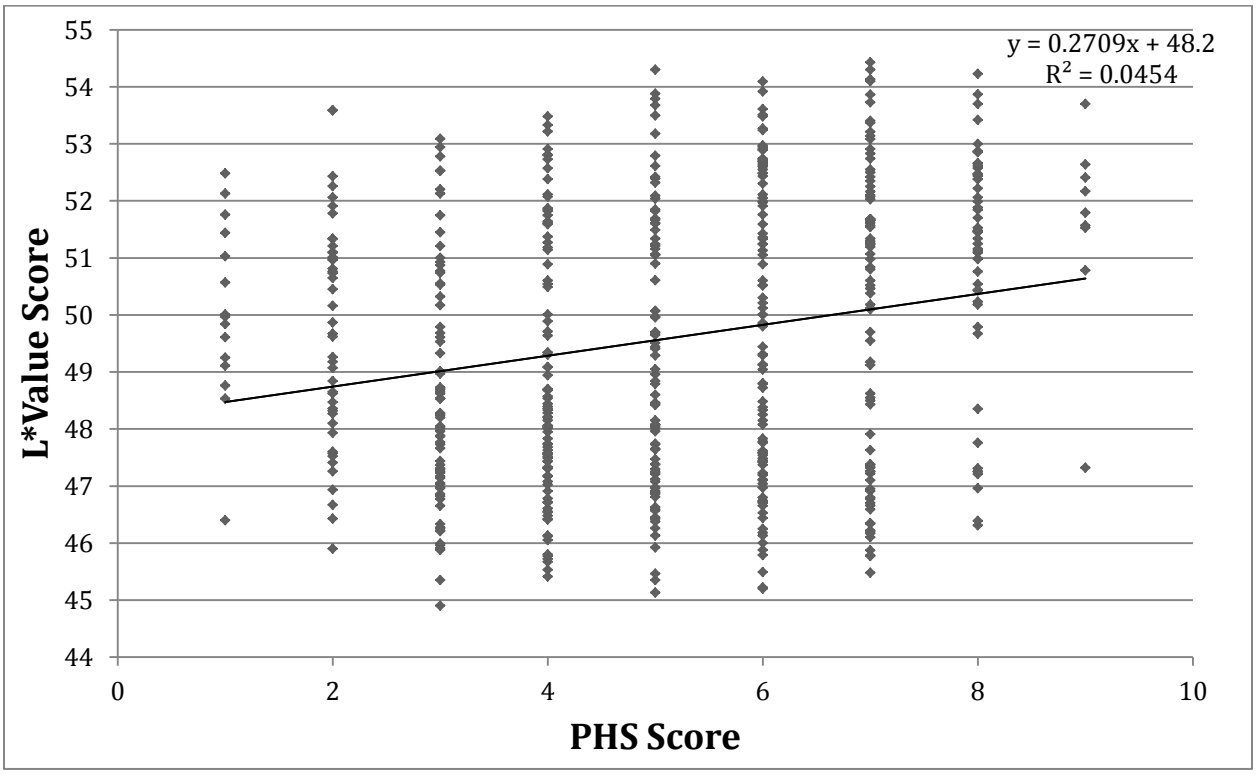

Fig. 3. Correlation analysis for PHS score and L* value evaluations across six North Dakota environments

There was a significant correlation between PHS and falling number readings across three environments. A significant negative correlation was calculated between PHS and falling numbers readings at the 2006 Casselton, and 2008 Casselton and Carrington environments. Falling number readings may be indicative of PHS; however, the readings are not always predictive of PHS. Singh et al. (2008) illustrated that some wheat genotypes exhibiting high falling numbers were also susceptible to sprouting. Additionally Barbeau et al. (2006) suggested that falling number should not be used as the sole criteria for determining the degree of sprout damage because it does not quantify or accurately reflect changes in protein composition and quality due to grain weathering.

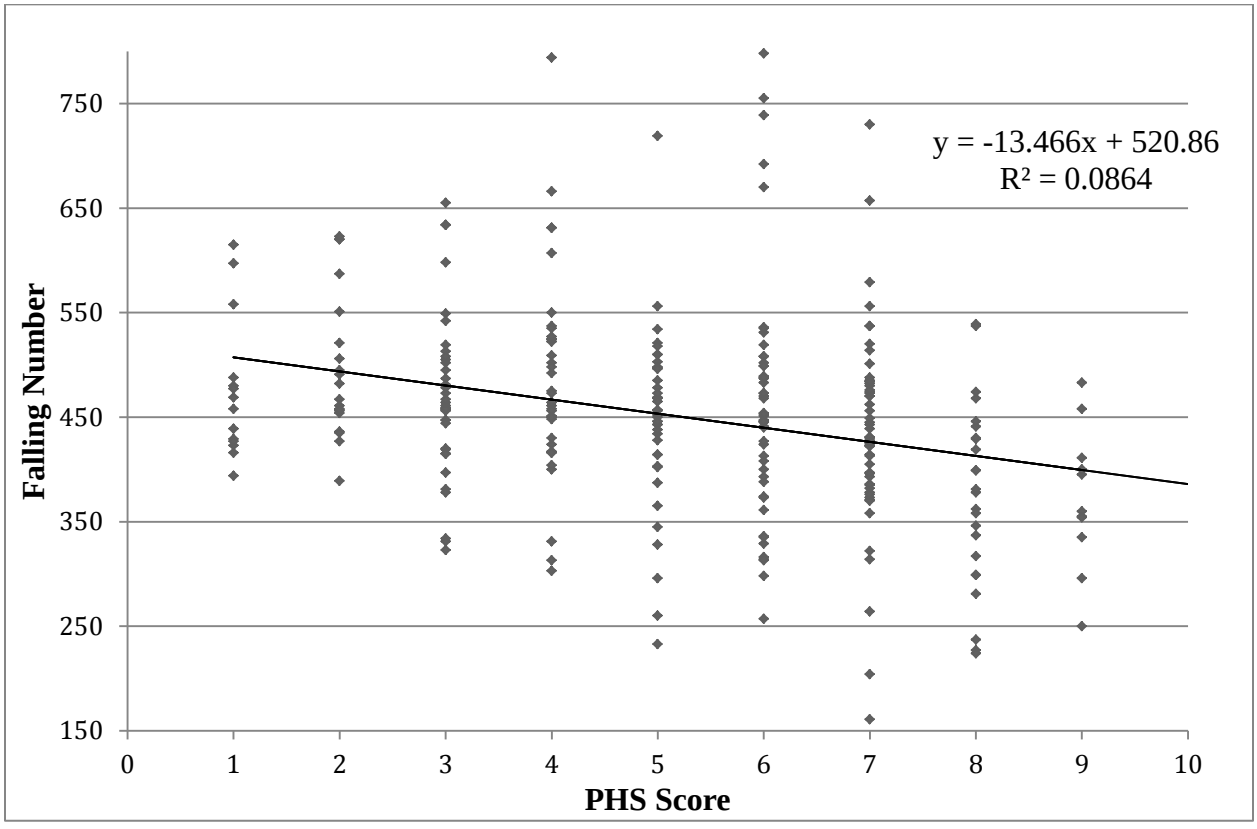

Fig. 4. Correlation analysis for PHS score and falling number values across three North Dakota environments over 2006, and 2008.

Glenn displayed a lower than average falling number value when compared with other red wheat genotypes (Table 16). However, Glenn did exhibit higher levels of tolerance to PHS (Table 12), which is an example of why falling number should not be used as the sole criteria for predicting PHS.

SUMMARY

Although both red and white kernel wheat genotypes exhibited a range of reactions when exposed to PHS conditions, the red genotypes in this study generally expressed a higher level of tolerance than white genotypes. Still, several white kernel genotypes were among the most tolerant to PHS. This indicates that the all genes controlling seed dormancy, or tolerance to PHS are not necessarily linked to the *R*-color alleles.

Environments that received less than average rainfall, and higher than average temperatures resulted in lower PHS scores than those that had lower temperatures and average to above average rainfall. Similarly, Biddulph et al, (2005) concluded that high temperatures and drought stress increase dormancy significantly.

Both red and white kernel genotypes had significantly different mean colorimeter L* values. Although some of the differences are likely due to environment, this may be indicative of differences in seed color genotype, particularly for the red kernel genotypes. Prior knowledge of the seed color genotype of every line and cultivar was not available, and the lines and cultivars were not genotyped for the color alleles as part of these experiments.

There were significant genotype differences for falling number, and while all falling number readings for genotypes were above the minimum considered indicative of PHS, the white kernel genotypes generally exhibited lower falling number readings than the red. Also, a negative correlation was calculated between PHS scores and falling number readings, which suggests that falling number readings are not always indicative or predictive of PHS.

Yield and test weight data comparisons between red and white kernel genotypes suggest that in general, the red genotypes are more highly adapted to the region. This could be reflective of the fact that the breeding and development of white wheat genotypes for the region is more

recent. Still, several white wheat genotypes were not only as tolerant or more tolerant than the red spring wheat genotypes, but several were highly competitive for grain yield and test weight, which are traits producers value in spring cultivars that are grown in the Northern Plains.

In summary, despite the general susceptibility of white kernel genotypes to PHS, there are several white genotypes tolerant to PHS that also exhibit adequate adaptation to the region. Breeders should consider the use of these as parents when developing white wheat genotypes for the region. Furthermore, falling number readings should not be used as the only indicator or predictor of PHS, and breeders should consider both the impact of genotype and environment on the phenotype when attempting to select for optimal white kernel color.

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